Research Article

Native and non-native unionids respond differently to the presence of fouling dreissenid mussels

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Abstract

Unionid mussels are globally threatened by several human disturbances, including the introduction of non-native species. Among these, biofouling zebra and quagga mussels of Ponto-Caspian origin are considered to be especially detrimental to unionid locomotion, filtration and physical condition. The aim of our study was to determine and compare the impact of dreissenid fouling and/or presence on locomotion and burrowing of the native *Unio tumidus* and invasive *Sinanodonta woodiana*, a novel invader expanding its range in Europe in recent decades. We tested unionids collected from Lake Balaton (central Europe) that were fouled by dreissenids (zebra and quagga mussels mixed), cleaned of fouling or non-fouled (collected without any signs of dreissenid fouling). Moreover, unionids were tested in the presence or absence of other fouled individuals and dreissenids isolated in mesh bags to determine the influence of direct fouling and presence of dreissenids in the environment on unionid behaviour. Movement initiation time, locomotion distance and burrowing level were retrieved from videos recorded for 24 hours. Direct fouling affected only the behaviour of *U. tumidus*, limiting their burrowing and delaying movements. After removal of fouling, movement timing returned back to normal, but mussels still burrowed less than the control non-fouled individuals, indicating persisting effects of fouling on physical condition. Moreover, *U. tumidus* reduced their locomotion in the presence of fouled unionids. *Sinanodonta woodiana* responded to the presence of dreissenids (especially quagga mussels) with increased burrowing. These different responses of the two unionid species to *Dreissena* spp. indicate that biofoulers may influence biotic interactions between the unionids by promoting the invasive species (less susceptible to negative effects of fouling). Moreover, *S. woodiana* may indirectly affect *U. tumidus* through apparent competition, constituting an environmental reservoir of biofoulers exerting a stronger impact on the native species.

Key words: Biofouling, biological invasions, Bivalvia, burrowing, ecosystem engineers, interspecific interactions, locomotion, *Sinanodonta woodiana*, *Unio tumidus*, Unionidae

Introduction

Bivalves are ecosystem engineers altering ecosystem structure and function by increasing water clarity and modifying the bottom quality (Strayer et al. 1999; Karatayev et al. 2002; Sousa et al. 2009). Their reported effects consist in declines in plankton abundance (Kissman et al. 2010; Karatayev et al. 2023), decreases in

young fish survival (Irwin et al. 2009), changes in fish feeding patterns (Mayer et al. 2001; Balogh et al. 2022), increases in benthic invertebrate abundance (Novais et al. 2015; Ilarri et al. 2018), and development of submerged aquatic vegetation (Chu et al. 2004; Zhu et al. 2006), resulting in a more benthic-oriented food web structure (Mills et al. 2003; Miehls et al. 2009).

Bivalve species richness and abundance decrease all over the world due to on-going climate change, increasing water pollution and habitat destruction (Strayer and Malcom 2007). This particularly applies to freshwater mussels of the family Unionidae, with dozens of already extinct species and hundreds more heavily endangered (Aldridge et al. 2023; Sousa et al. 2023). Due to their important environmental functions and ecosystem services they provide, further unionid extinction may lead to irreversible changes and effects on the entire aquatic community (Vaughn 2018; Zieritz et al. 2022).

One of the greatest threats to native unionid mussels is the spread of invasive mussel species (Gutiérrez et al. 2014; Douda et al. 2024), including biofouling dreissenids: the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and the quagga mussel *Dreissena rostriformis bugensis* Andrusov, 1897. The dreissenids, originating from the Ponto-Caspian region (catchments of the Black, Azov and Caspian Seas and lowland parts of the inflowing rivers) have successfully invaded freshwater ecosystems in Europe and North America (Matthews et al. 2014; Collas et al. 2018). *Dreissena polymorpha* has spread in Western Europe since the beginning of the 19th century (Harzhauser and Mandic 2010), whereas *D. r. bugensis* started to spread in the 20th century (Therriault et al. 2005) and its invasion is ongoing on both continents. This has led to the co-occurrence of both species in more and more invaded locations (Zhulidov et al. 2004; Grutters et al. 2012).

Dreissena spp. rapidly develop large populations and settle on unionids in high numbers, especially when other hard substrata are scarce, and the mass of fouling dreissenids can exceed the biomass of their host (Burlakova et al. 2000). This impairs physiological condition of unionids, as *Dreissena* spp. can block their siphons preventing them from filtering and therefore breathing and feeding (Ricciardi et al. 1996; Sousa et al. 2011; Bódis et al. 2014). Dreissenids can also inhibit unionid locomotion (Van Appledorn and Bach 2007) and/or burrowing, making them vulnerable to unfavourable environmental conditions or predation (Saloom and Duncan 2005). In addition, they may compete for food with the unionids, causing severe declines in phytoplankton (Higgins and Zanden 2010). As a result, the spread of *Dreissena* species may further endanger or lead to extinction of already threatened unionid species (Ricciardi and Whoriskey 2004).

An exception in the generally endangered Unionidae family is the invasive Chinese pond mussel *Sinanodonta woodiana* (Lea, 1834), native to Eastern Asia (Lopes-Lima et al. 2020), but in recent decades (since 1959) spreading in Europe (Douda et al. 2024). This is a fast-growing and fast-reproducing (Douda et al. 2021) species of high ecological plasticity, tolerant to wider ranges of environmental conditions in comparison to native European Unionidae (Kraszewski and Zdanowski 2007; Poznańska-Kakareko et al. 2021; Zieritz et al. 2021; Dobler et al. 2022). It can co-occur with native mussels and outcompete them for food, fish hosts for their larvae, and living space (Douda and Čadková 2018).

Both native and invasive Unionidae are commonly fouled by dreissenids (Bódis et al. 2014; Balogh et al. 2024). Dreissenids can interfere with the invasion of *S. woodiana*, with the final outcome depending on the relative susceptibility of *S. woodiana*

and native unionids to fouling and its effects (Bódis et al. 2014). High vulnerability of the invasive *S. woodiana* to fouling would negatively affect its establishment in areas occupied by dreissenids, whereas its resistance would facilitate competitive exclusion of other unionid species (Sousa et al. 2011). Therefore, the aim of our study was to determine and compare the effects of fouling and/or presence of the invasive mussels *D. r. bugensis* and *D. polymorpha* (responses to own fouling, to the presence of fouled conspecifics and to the presence of dreissenids on other substratum in the environment) on the locomotion and burrowing of two unionid mussels: the native *Unio tumidus* Philipsson, 1788 and the invasive *S. woodiana*. These species often co-occur in areas invaded by *S. woodiana* in Europe (e.g. in Lake Balaton; Benkő-Kiss et al. 2013) and can interact with each other, which can be additionally modulated by biofouling. For our study, the mussels were collected from a single location in Lake Balaton (Hungary) to make sure that potential differences in local living conditions of particular species would not affect the results. We hypothesized that: (1) fouling reduces unionid locomotion and burrowing; (2) this effect can be purely mechanical (only when the fouling is directly present), or (3) can persist after fouling removal (due to worsened physiological condition of the host). Additionally, we hypothesized that (4) unionids can detect and respond by behaviour to chemical cues released by other unionids fouled by dreissenids or directly by *Dreissena* spp. individuals.

Materials and methods

Mussel collection in the field

We collected all mussels manually (randomly by hand) or using a Surber net from Lake Balaton in Keszthely, Hungary (46°46'11"N, 17°14'53"E) in summer 2022. Lake Balaton, the largest lake in Central Europe, had been an isolated water body until the opening of the Sió Canal, which created conditions for the spread of invasive species from the River Danube (Benkő-Kiss et al. 2013). This eutrophic, shallow, and mainly muddy lake provides an opportunity to collect all the mussel species at one site: *S. woodiana* (temperate lineage from Eastern Asia) (Douda et al. 2024) has been present in the lake since 2006 (Benkő-Kiss et al. 2013), zebra mussels since 1932 (Sebestyén 1938) and quagga mussels since 2008 (Balogh et al. 2018). We collected *S. woodiana* and *U. tumidus* from sandy/muddy bottom at a water depth of 0.5–1 m. Some individuals were fouled with a mixture of both *Dreissena* species, whereas others were clean (without any marks of fouling). *Dreissena polymorpha* to *D. r. bugensis* ratio on unionid mussels at the collection site is ca. 3:2 (Balogh et al. 2024). We transported the mussels in buckets (containing sand and water from the collection place) to the laboratory in the Balaton Limnological Research Institute (Tihany, Hungary), where, after two weeks of acclimation, we conducted the experiments. We did not observe any mortality during this time. After completing all the tests, the mussels were weighed and measured (Table 1). We determined the mass of the *Dreissena* spp. fouling on each unionid considering it as a whole, without separating the dreissenid species. We assumed that the total fouling mass has the greatest effect on the fouled animal, irrespective of the fouling species, individual size and numbers. The fouling to host mass ratios were similar for both unionid species (Table 1) and indicated moderate level of fouling (20% of the host mass) compared to other environments, where the total fouling mass may even exceed that of their host (Burlakova et al. 2000; Dzierżyńska-Białończyk et al. 2018a).

Table 1. Weight and length of native and invasive mussels used in experiments. Underlying data are available in Suppl. material 1.

	S. woodiana			*U. tumidus*		
	mean	**SD**	**range**	**mean**	**SD**	**range**
Wet mass (g)	149.4	46.4	52.4–285.0	41.4	8.3	18.8–64.6
Length (mm)	107.1	10.9	78–129	68.2	5.5	56–83
Dreissena spp. mass (g)	27.0	11.5	10.5–50.0	7.5	4.6	4.0–20.4
Dreissena / unionid mass ratio	0.20	0.08	0.06–0.33	0.17	0.08	0.09–0.32

SD – standard deviation.

Laboratory conditions

The laboratory with stock and experimental tanks was equipped with air conditioning to stabilise water temperature. Unionids, each species as well as fouled and non-fouled individuals separately, were stocked in aerated and filtered flow-through 250-L tanks supplied with fresh water from the lake (flow rate: 30 L/h). Water parameters in the stock and experimental tanks were measured with a multimeter Multi340i (WTW, Weilheim, Germany) (Table 2). The mussels were fed with cultured *Scenedesmus* sp. suspension at a concentration of 5 mg L^{-1} (Douda and Čadková 2018) three times a week, also between the replicates of the experiments.

Table 2. Water parameters in the stock and experimental tanks (lake water).

	Oxygen concentration [mg/mL]	**Oxygen saturation [%]**	**Temperature [°C]**	**pH**	**Conductivity [µS/cm]**
Stock tanks					
Mean	8.90	98.33	19.26	8.60	855.67
SD	0.27	1.86	0.32	0.03	10.12
Range	8.73–9.21	96.6–100.3	18.94–19.57	8.57–8.63	844–862
Experimental tanks					
Mean	6.34	69.28	18.65	8.14	853.50
SD	0.49	5.22	0.30	0.21	21.33
Range	5.04–6.75	55.7–74.3	18.28–18.97	7.77–8.39	811–871

SD – standard deviation.

Experimental setup

Direct impact of *Dreissena* spp. fouling on unionid behaviour (Experiment 1) was tested in 30 × 30 × 30 cm tanks, containing 10 cm of sand (sifted and rinsed) covered by 10 cm layer of lake water. To each tank, we introduced 4 mussels: two individuals of *S. woodiana* and two individuals of *U. tumidus* (to mimic their co-existence in the field) (Fig. 1). The mussel behaviour was recorded for 24 h with CCTV video-cameras (Samsung SNB-6004, South Korea) equipped with infrared illumination (LIR-CS32, IRLAB, Taiwan) enabling night-time observations. We used several mussel variants depending on their fouling status and processing in the laboratory. Their full descriptions and explanations of use are presented in Table 3.
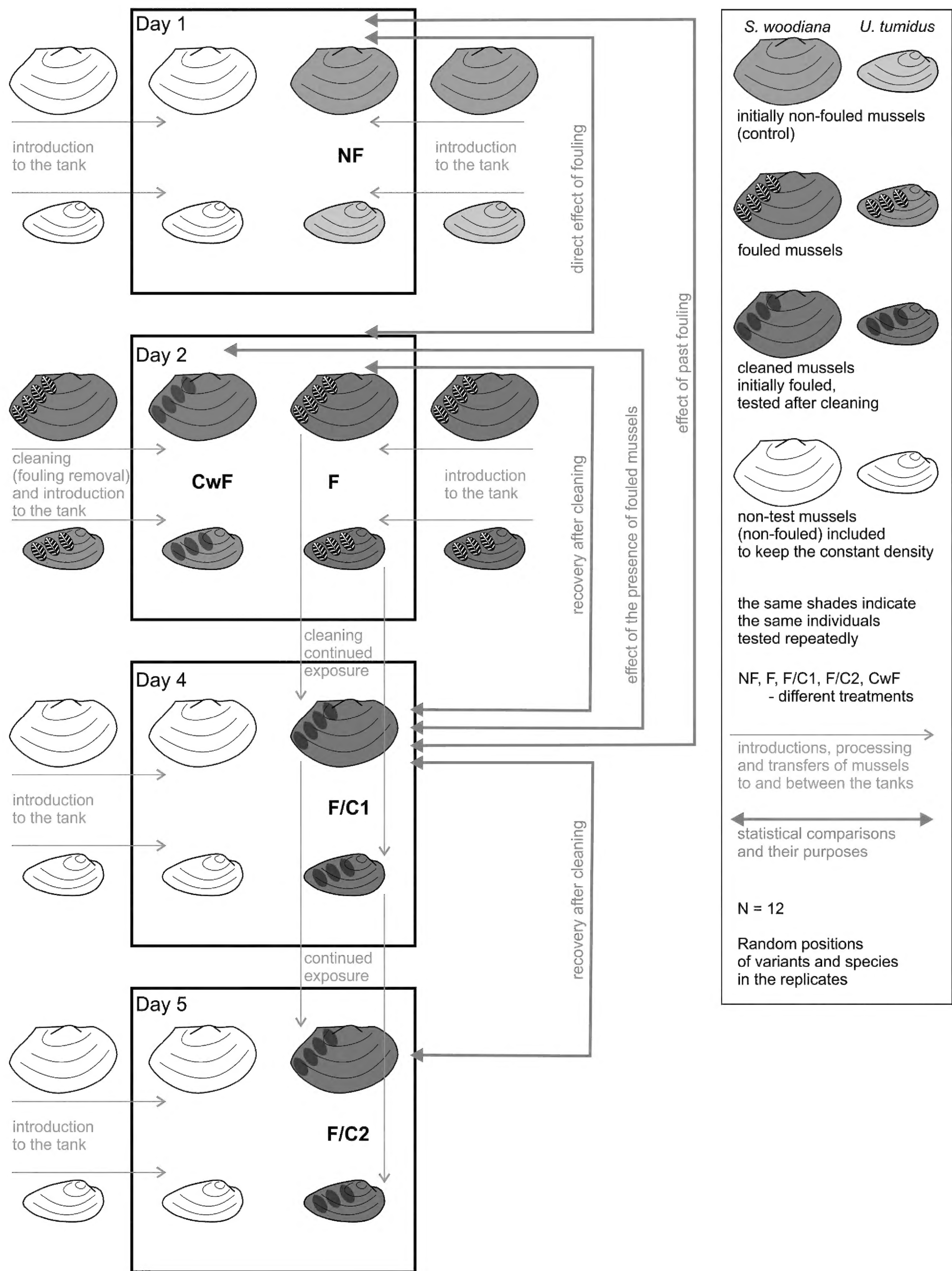
Figure 1. Mussel arrangement in the experimental tanks of Experiment 1 on the effect of *Dreissena* spp. fouling on the behaviour of *S. woodiana* and *U. tumidus*. See Table 3 for detailed explanations of variants (NF, F, F/C1, F/C2, CwF).

Table 3. Full list of variants and their comparisons in Experiment 1 with explanations of their purposes. See Fig. 1 for variant arrangements in the experimental tanks. In variants F, F/C1 and F/C2, we used the same individuals tested repeatedly.

Variants			Description	Purpose
NF (non-fouled)			Control; non-fouled unionids collected in the field without any trace of fouling on their shells	Control for the fouling variants (fouled F and cleaned F/C1)
F (fouled)			Fouled unionids tested with their fouling	To determine the direct impact of dreissenids fouling on mussel behaviour (compared to NF)
F/C1 (cleaned, time 1)			F unionids cleaned of fouling and tested for the second time two days after cleaning (with no dreissenids in the tank)	To determine whether the behaviour of mussels would change after the removal of fouling (compared to F) and whether it would return back to normal (compared to NF)
F/C2 (cleaned, time 2)			F/C1 unionids tested once again on the next day (for the third time in general, second time without fouling)	To check whether the repeated testing of mussels and passing time has an impact on their behaviour (compared to F/C1)
CwF (cleaned with fouled)			Unionids collected in the field as fouled, cleaned of fouling and tested two days after cleaning in the presence of other, fouled unionids (from variant F)	To determine whether the presence of other fouled unionids has an impact on their behaviour (compared to F/C1, exposed in the total absence of dreissenids)
Comparisons between the variants			**Purpose**	
NF	**vs**	**F**	To test the direct effect of fouling on unionid behaviour of both chemical cues and physical presence of biofoulers	
NF	**vs**	**F/C1**	To test the effect of past fouling on unionid behaviour (potentially deteriorated condition of mussels recently cleaned of fouling)	
F	**vs**	**F/C1**	To test the possibility of potential recovery from the past fouling with passing time	
F/C1	**vs**	**F/C2**	To test the potential effects of passing time on the responses of unionids exposed to the experimental conditions	
CwF	**vs**	**F/C1**	To test the unionid responses to the presence of fouled individuals in the environment (chemical cues from fouled unionids and biofoulers)	

First, we tested non-fouled mussels of variant NF (one *S. woodiana* and one *U. tumidus* individual per tank) accompanied by two additional non-fouled individuals (one per species) to have the total number of four individuals per tank. Then, we tested two fouled mussels (F) accompanied by two mussels cleaned two days before the exposure (CwF). After this exposure, fouled individuals (F) were cleaned and kept in tanks for two days. Then, they were exposed again (as F/C1) in the presence of two additional non-fouled mussels. On the next day, F/C1 mussels were exposed once again (as F/C2) in the presence of two additional non-fouled mussels. Thus, each experimental tank always contained four mussels, two of each species, in different fouling conditions (Fig. 1).

Effects of the presence of *Dreissena* spp. (Experiment 2) on unionid behaviour were tested in tanks prepared similarly as for Experiment 1. We introduced two cleaned (two days before the experiment) unionids (one *S. woodiana* and one *U. tumidus*) into each tank (one individual in the centre of each half of the tank bottom). We used cleaned mussels to be sure they had some past experiences with *Dreissena* spp. fouling. In one randomly selected corner of the tank, we placed a mesh bag with 50 individuals of *D. r. bugensis* (mean wet mass: 13.5–15 g) or *D. polymorpha* (12–12.5 g). Here, the two species of *Dreissena* spp. were tested separately, as, in contrast to the direct impact of the mass of attached individuals, we expected that unionids can respond differently to the remote presence of a particular fouler species. In parallel, we carried out control trials in tanks without mesh bags with dreissenids. Our Experiment 1 showed that the fouling *Dreissena* spp. mass of the magnitude used in Experiment 2 was capable of triggering behavioural responses of Unionidae (see Results).

All configurations were recorded for 24 hours in 12 replicates.

Data analysis

After completing the experiments, we analysed the obtained videos to determine: (i) movement initiation time (time from the introduction to the first activity, i.e. initiation of locomotion or burrowing), (ii) locomotion distance and (iii) mean burrowing level [%]. Every minute, we estimated the level of bivalve burrowing (using a 5-level percentage scale: 0, 25, 50, 75 and 100%) based on the length of the part of the shell below the substratum surface to the total shell length (according to Poznańska-Kakareko et al. 2021). Mean burrowing level was calculated according to the formula:

$$MB = \sum_{i=1}^{4} \left[25\% * it_i \right] / \sum_{i=0}^{4} t_i \qquad (1)$$

where: i – burrowing level: 5 steps ranging from 0 (totally exposed on the surface) to 4 (fully burrowed); t_i – time spent by the mussel at burrowing level i.

The list of all comparisons between the variants of Experiment 1 is presented in Table 3. As the data strongly violated normality and homoscedasticity assumptions (tested with Shapiro-Wilk and Levene tests, respectively), we used non-parametric Mann-Whitney U tests to compare mussel behaviour in experimental treatments, except for the comparisons among F-F/C2 variants of Experiment 1, where the same individuals were tested several times. For those, we used Wilcoxon signed rank tests for paired samples. In Experiment 2, we compared unionid behaviour in *Dreissena* sp. presence treatments to control treatments using Mann-Whitney tests to check unionid responses to the presence of biofoulers (chemical cues from biofoulers only). We applied a sequential Bonferroni correction for multiple comparisons (within each variable and species). However, we decided to report and interpret results both with and without the correction, as it is commonly considered as overly conservative with a large number of comparisons (Moran 2003). Statistical analyses were carried out using SPSS 29.0 (IBM Inc.).

Results

Experiment 1: Unionid responses to direct *D. r. bugensis* and *D. polymorpha* fouling and presence of fouled unionids

There was no significant effect of *Dreissena* spp. fouling on *S. woodiana* movement initiation time and locomotion (Fig. 2a, e). Mean burrowing level of cleaned *S. woodiana* (variant F/C1) was reduced compared to the control individuals (NF) but increased again after a longer exposure (F/C2) (Fig. 2g, Table 4).

For *U. tumidus*, we noted differences in movement initiation time: fouled mussels (F) started to move later compared to control non-fouled individuals (NF). When the fouled *U. tumidus* (F) were cleaned (becoming F/C1), they hastened their movement initiation time up to the level exhibited by the control individuals (NF). Moreover, cleaned *U. tumidus* (CwF) exposed in the company of fouled individuals started to move later (general activity) compared to *U. tumidus* kept in the absence of dreissenids (F/C1) and did not move horizontally at all (Fig. 2b, f, Table 4). *Unio tumidus* burrowed less when fouled (F) compared to the control non-fouled individuals (NF), and this effect persisted after cleaning (F/C1) (Fig. 2h, Table 4).

Table 4. Unionid responses to direct *D. r. bugensis* and *D. polymorpha* fouling and presence of fouled unionids in Experiment 1. Variant NF: mussels collected in the field without any trace of fouling on their shells, hereafter referred to as non-fouled mussels; variant F: mussels collected as fouled by *Dreissena* spp. and tested first time with their own fouling (fouled mussels); variant F/C1: F mussels, cleaned and tested after two days in the presence of non-fouled individuals (cleaned mussels); variant F/C2: F/C1 mussels tested on the next day (for the third time); variant CwF: mussels collected as fouled, cleaned two days before testing, and tested in the presence of fouled individuals. Variants NF vs F and F vs CwF were compared with Mann-Whitney U tests; variants F-F/C2 were compared to each other using Wilcoxon signed rank tests for paired data. Statistically significant differences are marked with asterisks and those that are still significant with the sequential Bonferroni correction are marked in bold font. Z – test statistic; P – statistical significance. Underlying data are available in Suppl. material 1.

Variable	Configurations			S. woodiana		U. tumidus	
				z	P	z	P
Movement initiation time	Non-fouled (control, NF)	vs.	Fouled (F)	−0.69	0.488	−2.42	0.015*
	Non-fouled (control, NF)		Cleaned (F/C1)	−0.55	0.583	−1.21	0.225
	Fouled (F)		Cleaned (F/C1)	−0.16	0.875	−2.98	**0.003***
	Cleaned (F/C1)		Cleaned (F/C2)	−0.16	0.875	−1.14	0.255
	Cleaned (CwF)		Cleaned (F/C1)	−0.40	0.686	−2.02	0.043*
Locomotion distance	Non-fouled (control, NF)	vs.	Fouled (F)	−0.79	0.429	−0.04	0.970
	Non-fouled (control, NF)		Cleaned (F/C1)	−0.41	0.684	−0.72	0.470
	Fouled (F)		Cleaned (F/C1)	−0.52	0.600	−0.34	0.735
	Cleaned (F/C1)		Cleaned (F/C2)	−0.85	0.398	−0.42	0.674
	Cleaned (CwF)		Cleaned (F/C1)	−0.41	0.684	−2.44	0.015*
Mean burrowing level	Non-fouled (control, NF)	vs.	Fouled (F)	−0.43	0.665	−3.12	**0.002***
	Non-fouled (control, NF)		Cleaned (F/C1)	−2.54	0.011*	−2.94	**0.003***
	Fouled (F)		Cleaned (F/C1)	−1.18	0.239	−0.63	0.530
	Cleaned (F/C1)		Cleaned (F/C2)	−2.04	0.041*	−1.88	0.060
	Cleaned (CwF)		Cleaned (F/C1)	−1.79	0.073	−0.17	0.862

Neither species showed significantly different movement initiation times or locomotion parameters exclusively due to passing time (comparison of F/C1 vs F/C2).

Experiment 2: Unionid responses to waterborne cues of *D. r. bugensis* and *D. polymorpha*

Sinanodonta woodiana showed a higher mean burrowing level in the presence of *D. r. bugensis* compared to the control (Fig. 3, Table 5). Neither the presence of *D. r. bugensis* nor *D. polymorpha* affected the locomotion and burrowing of *U. tumidus* (Fig. 3, Table 5).

Discussion

Consistently with our first hypothesis, dreissenid fouling affected the behaviour of unionid mussels. *Sinanodonta woodiana* responded only with changed burrowing level. In Experiment 1, we observed shallower burrowing of *S. woodiana* immediately after fouling removal, but, over time, burrowing returned to the level exhibited by the control, non-fouled mussels. On the other hand, in Experiment 2, *S. woodiana* burrowed deeper in the presence of quagga mussels compared to the control. This might be a defensive response of *S. woodiana* to
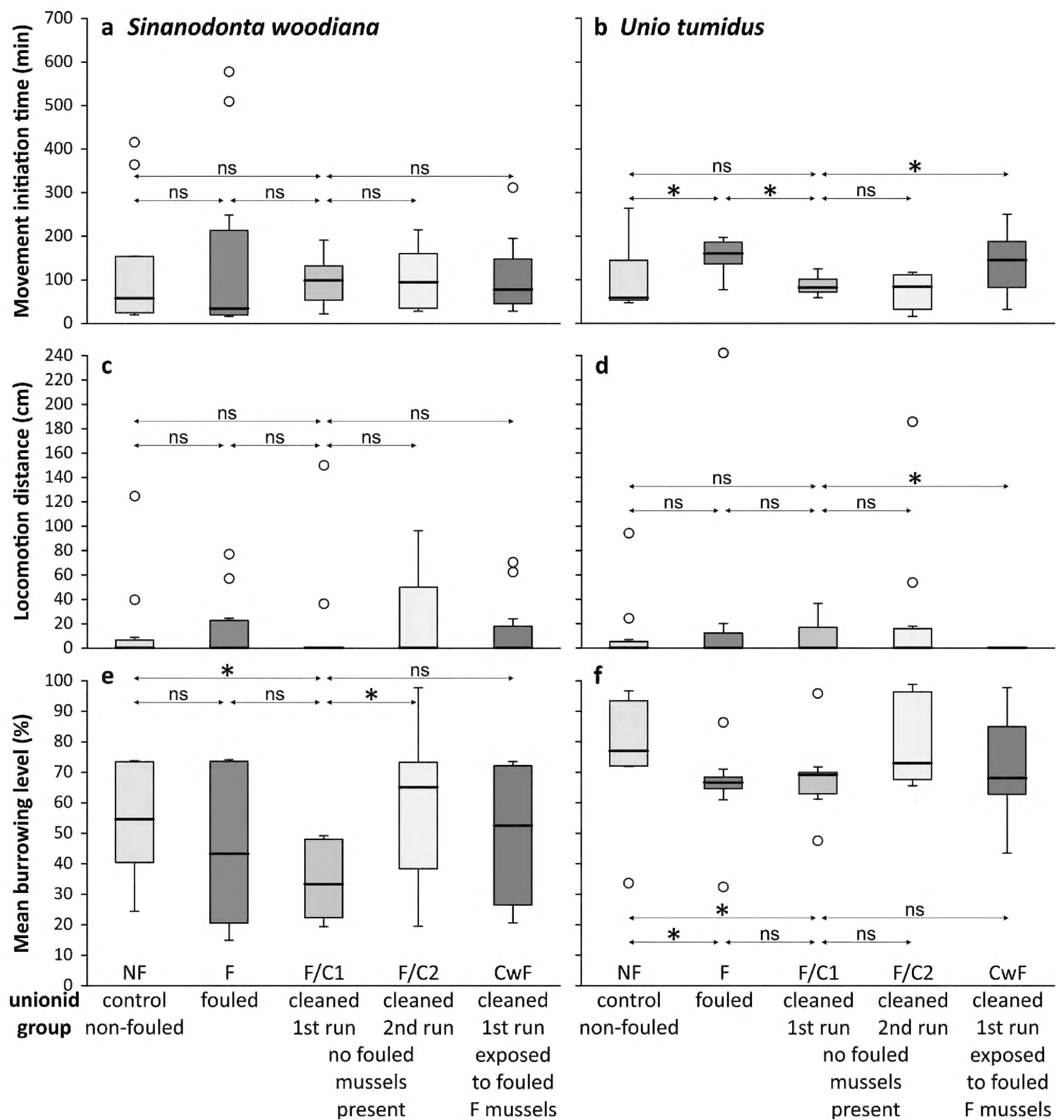
Figure 2. Unionid responses to the direct dreissenid fouling and presence of fouled unionids in Experiment 1: **a, b** movement initiation time [min] **c, d** locomotion distance [cm] **e, f** mean burrowing level [%]. Asterisks mark significant differences between the variants (ns – non-significant). Boxplots present medians (horizontal lines), 1st and 3rd quartiles (top and lower boxes, respectively), 1.5*interquartile range (whiskers) and outliers (circles). Variant NF: mussels collected in the field without any trace of fouling on their shells, hereafter referred to as non-fouled mussels; variant F: mussels collected as fouled by *Dreissena* spp. and tested first time with their own fouling (fouled mussels); variant F/C1: F mussels, cleaned and tested after two days in the presence of non-fouled individuals (cleaned mussels); variant F/C2: F/C1 mussels tested on the next day (for the third time); variant CwF: mussels collected as fouled, cleaned two days before testing, and tested in the presence of fouled individuals.

the presence of dreissenids, consisting in increased burrowing. It is worth noticing that a similar, though marginally non-significant tendency for increased burrowing was observed in *S. woodiana* exposed to fouled unionids (variants CwF vs F/C1, Fig. 2, Table 4).
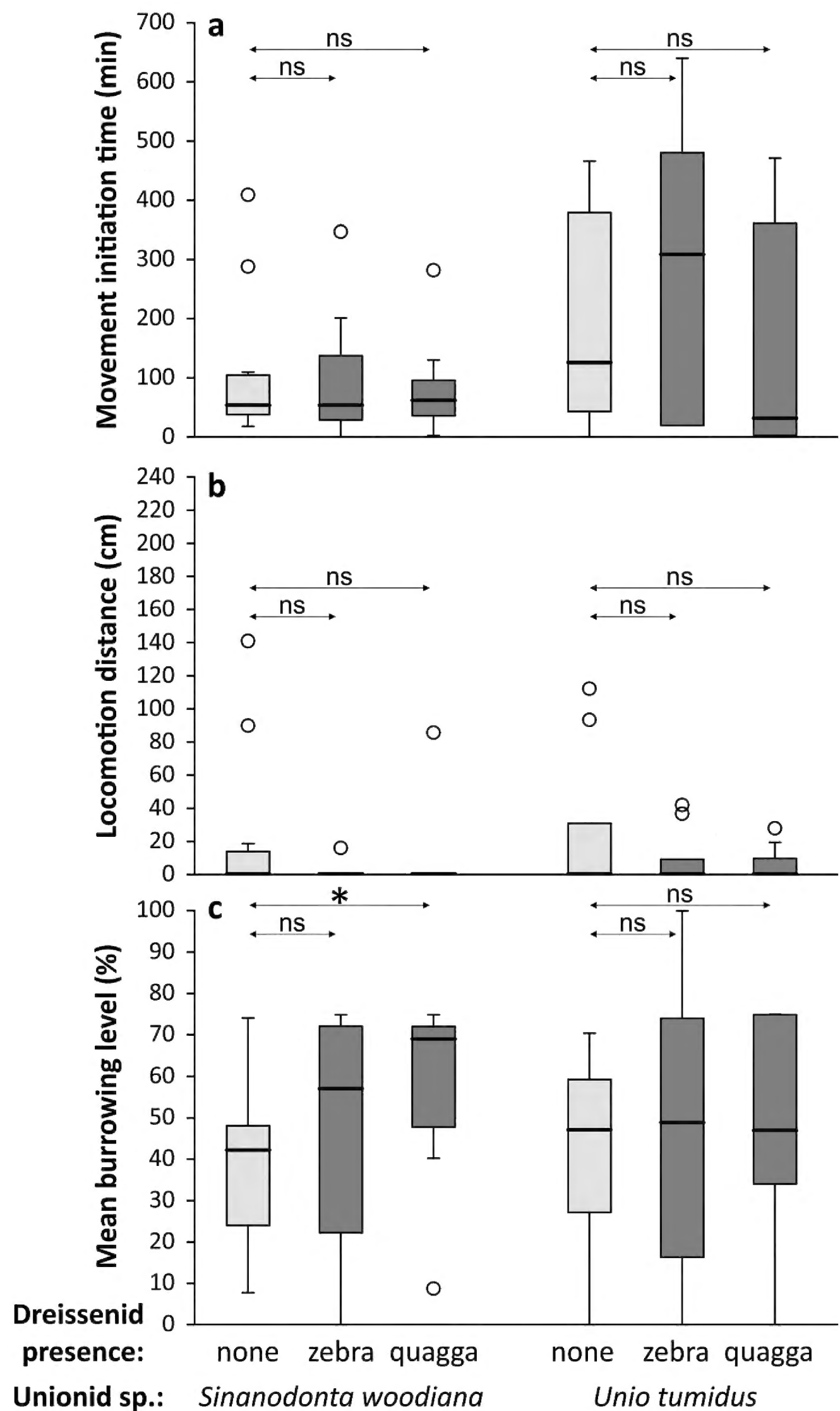
Figure 3. Unionid responses to *D. r. bugensis* and *D. polymorpha* waterborne cues in Experiment 2. Asterisks mark significant differences between the variants (ns – no significant). Boxplots present medians (horizontal lines), 1st and 3rd quartiles (boxes), 1.5*interquartile range (whiskers) and outliers (circles).

The pattern observed for *S. woodiana* in Experiment 1 can be explained by contrasting effects of fouling (mechanical obstacle to efficient burrowing) and defensive responses to *Dreissena* spp. presence (stimulating burrowing). For fouled individuals, burrowing was more difficult, but they kept trying to defend themselves from fouling, resulting in a similar level as that showed by the control mussels.

Table 5. Unionid responses to *D. r. bugensis* and *D. polymorpha* waterborne cues in Experiment 2: compared to their behaviour on the control (pairwise Mann-Whitney U test). Statistically significant differences are marked with asterisks (note that they do not pass the Bonferroni correction for multiple comparisons). z – test statistic; P – statistical significance. Underlying data are available in Suppl. material 1.

Variable	Configurations			*S. woodiana*		*U. tumidus*	
				z	P	z	P
Movement initiation time	control	vs.	*D. polymorpha* presence	−0.37	0.712	−0.60	0.545
			D. r. bugensis presence	−0.17	0.862	−0.90	0.369
Locomotion distance	control	vs.	*D. polymorpha* presence	−1.12	0.264	−0.60	0.551
			D. r. bugensis presence	−1.11	0.266	−0.47	0.636
Mean burrowing level	control	vs.	*D. polymorpha* presence	−1.10	0.273	−0.30	0.762
			D. r. bugensis presence	−2.14	0.033*	−0.98	0.327

Immediately after the fouling removal, with no dreissenids present in the environment (variant F/C1, no need for anti-fouling defence), they burrowed more shallowly due to recently experienced problems related to fouling (e.g. exhaustion), but, with time (the next experimental round, F/C2), their burrowing returned to the control level. Nevertheless, this effect of fouling persisting after cleaning, though short-timed, suggests that the impact of dreissenids on their hosts was not purely mechanical, but also affected their condition.

Increased burrowing is a natural defence mechanism (Saloom and Duncan 2005) and may indicate an attempt to avoid fouling mussels, which, once attached, could have a more negative impact on their host condition than when acting only indirectly by their presence nearby (Sousa et al. 2011). Mussels are known to sense the presence of predators (Reimer and Harms-Ringdahl 2001; Meira et al. 2024) and parasites (Selbach and Mouritsen 2020) from chemical cues in the environment, as well as detect alarm signals from damaged conspecifics (Leonard et al. 1999), which results in the induction of various defence mechanisms, such as increased burrowing (Griffiths and Richardson 2006). The occurrence of a defence mechanism in *S. woodiana* may give this species an advantage in unfavourable conditions, such as the presence of biofouling *Dreissena* spp. The deeper the mussel burrows, the less exposed its shell is to the fouling dreissenids, which directly affects the degree of fouling, as shown by Urbańska et al. (2019). Moreover, existing fouling can also be reduced by the burrowing of the host unionid, as dreissenids are known to detach from unsuitable (e.g. burrowed) substrata and move in search of a better attachment site (Dzierżyńska-Białończyk et al. 2018b; Balogh et al. 2024). Dzierżyńska-Białończyk et al. (2018a) and Balogh et al. (2024) have shown that burrowed *S. woodiana* (but not the native unionid species, including *U. tumidus*) were less fouled by dreissenids than individuals exposed on the surface, confirming a defensive potential of this behaviour.

In Experiment 2, *S. woodiana* responded significantly only to the presence of quagga mussels, which confirmed that unionids can detect and respond to chemical cues of other bivalves in the environment (our fourth hypothesis). However, it should be noted that a similar tendency was also apparent in the presence of zebra mussels, thus the support for the hypothesis that unionid responses to fouling depended on the fouler species remains weak. Anyway, it is possible that *S. woodiana* is more familiar with quagga mussels, which are more abundant in Lake Balaton, although this ratio may vary in different parts of the lake (Balogh et al. 2008; Balogh et al. 2024). Moreover, quagga mussels are less associated with their

substratum (D'Hont et al. 2021) and easier to detach due to their weaker adhesion strength (Balogh et al. 2019), thus burrowing can be a more effective defence mechanism against them compared to more strongly and more permanently attached zebra mussels.

In Experiment 1, fouled *U. tumidus* showed a delayed movement initiation time and shallower burrowing compared to the control, non-fouled individuals. After the fouling removal, the movement initiation time of *U. tumidus* (variant F/C1) returned to the control level, but the burrowing remained weakened. Therefore, changes in the behaviour of *U. tumidus* were driven by the mechanical effect of fouling present on their shells, as well as by the impaired condition of fouled mussels. This supported our third hypothesis, as the fouling effect persisted after the fouling removal.

We did not observe any effects of direct fouling on the locomotion, in contrast to Van Appledorn and Bach (2007) working on North American unionids *Ligumia nasuta* Say, 1817 and *Anodonta grandis* Say, 1829. However, in accordance with our fourth hypothesis, *U. tumidus* responded to the presence of other fouled individuals by stopping any horizontal movements and delayed movement initiation (here: burrowing start, as locomotion did not occur at all) (CwF vs F/C1). Theoretically, this difference might be an artefact resulting from the fact that mussels from F/C1 were tested in the experimental arena for the second time, whereas for those from CwF it was the first experimental round. However, the comparison between animals tested repeatedly in consecutive experimental rounds under the same conditions (F/C1 vs F/C2) showed no significant differences and symptoms of exhaustion or habituation due to repeated testing, thus this explanation seems unlikely. On the other hand, the observed responses of *U. tumidus* to the presence of fouled individuals may represent a general reaction to stressed (here: fouled) conspecifics secreting some infochemicals indicating stressful environmental conditions. Definitely, *U. tumidus* did not respond to direct cues from dreissenids, as shown by Experiment 2.

All changes in the behaviour of *U. tumidus* induced by fouling or nearby presence of fouled individuals seem negative, exposing them to a number of environmental threats, including predation, parasites, dislodgement by water movements, desiccation during droughts, and further fouling by dreissenids (Bowers et al. 2005; Lymbery et al. 2021).

Our study showed that the behaviour of the native *U. tumidus* in the presence of fouling *Dreissena* spp. mussels was modified to a higher extent than that of the invasive *S. woodiana*. Moreover, the responses of *S. woodiana* appeared to have defensive and preventive effects against dreissenid fouling, whereas the behaviour of *U. tumidus* seemed to be impaired compared to their normal (control) activity. Thus, despite a similar relatively moderate level of fouling of both species in our study, dreissenids presence had stronger negative effects on *U. tumidus*. Due to large body size of *S. woodiana* and its weaker burrowing (Poznańska-Kakareko et al. 2021), more dreissenids, especially zebra mussels, can attach to and persistently stay on their surface than to smaller native mussels. Therefore, *S. woodiana* can act as a reservoir for dreissenids colonizing the native species, with the native species suffering more severe negative consequences of fouling. This suggests yet another potential effect of invasive dreissenids on native communities: their presence can influence interactions between native and invasive species of Unionidae, promoting the latter. On the other hand, *S. woodiana* can provide suitable substratum for dreissenid development. Moreover, we have shown that, beside parasites (McElwain 2019) and

predators (Meira et al. 2024), dreissenids can constitute another driver of apparent competition between invasive and native species, when the invader poses a threat to the native organism by increasing the abundance and availability of biofoulers. This effect is likely to be most pronounced in locations where shells of unionid mussels constitute the primary source of hard substratum available to dreissenids, such as soft lake bottoms, or dam reservoirs and river pools with limited flows and accumulated sediments, missing rocks and artificial embankments (Dzierżyńska-Białończyk et al., 2018a; Balogh et al. 2024). Nevertheless, such places are common in the environment and are frequently used by unionids. Therefore, dreissenid mussels can extend their distribution ranges as they are able to use their shells as attachment sites.

It should be noted that our research was conducted using mussels collected from a single location in Lake Balaton. This allowed us to eliminate potential confounding effects related to different conditions experienced by experimental animals before their sampling. We checked the situation taking place within the same natural community, living under the same conditions. However, we must admit that conducting the same research using mussels from other regions of the world may result in different results. To better understand the influence of dreissenids on Unionidae, it would be useful to conduct similar comparative studies with mussels from other lakes or rivers.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

KW: Conceptualisation, Methodology, Resources, Investigation, Formal analysis, Visualisation, Writing – Original draft, Writing – Review and Editing; CB: Conceptualisation, Methodology, Resources, Visualisation, Investigation, Writing – Review and Editing, Funding Acquisition; JK: Conceptualization, Methodology, Investigation, Validation, Formal analysis, Data Curation, Visualization, Writing – Review and Editing; DS: Methodology, Resources, Investigation, Writing – Review and Editing; ŁJ: Resources, Investigation, Writing – Review and Editing; MPK: Conceptualization, Methodology, Investigation, Validation, Visualization, Formal analysis, Supervision, Project administration, Writing – Review and Editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Dataset

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Data type: xlsx

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